

Evolution and Human Behavior

Evolution and Human Behavior 32 (2011) 21-28

Original Article

Mood and the speed of decisions about anticipated resources and hazards[☆] Elizabeth S. Paul^{*}, Innes Cuthill, Go Kuroso, Vicki Norton, Joe Woodgate, Michael Mendl

Centre for Behavioural Biology, University of Bristol, Bristol, UK Initial receipt 2 November 2009; final revision received 15 July 2010

Abstract

In addition to triggering appropriate physiological activity and behavioural responses, emotions and moods can have an important role in decision making. Anxiety, for example, arises in potentially dangerous situations and can bias people to judge many stimuli as more threatening. Here, we investigated the possibility that affective states may also influence the time taken to make such judgements. Participants completed the Positive and Negative Affect Schedule (PANAS) mood inventory [Watson, D., Clark, L.A., Tellegen, A. Development and validation of brief measures of positive and negative affect: the PANAS scales. *J Pers Soc Psychol*, 54 (1988) 1063–1070] and undertook a computer-based task in which they were required to decide whether ambiguous and unambiguous predictor stimuli heralded resources or hazards. While the two types of negative mood indicators measured by PANAS [high "negative activation" (high NA), a danger-oriented state such as anxiety, and low "positive activation" (low PA), a state related to loss or absence of opportunity, such as sadness] both biased decisions similarly towards expecting hazards and away from expecting resources, only individual variation in NA was associated with the speed at which these decisions were made. In particular, participants reporting higher NA showed a bias towards caution, being slower to decide that stimuli predicted hazards and not resources. These findings are discussed in terms of the "Smoke Detector Principle" in threat detection [Nesse, R.M. Natural selection and the regulation of defenses. A signal detection analysis of the smoke detector principle. *Evol Hum Behav*, 26 (2005) 88–105] and the potential value of speed–accuracy tradeoffs in the context of decision making in differing mood states, and the processes that might give rise to them.

© 2011 Elsevier Inc. All rights reserved.

Keywords: Mood; Affective state; Decision making; Speed-accuracy tradeoffs; Anxiety

1. Introduction

In the simplest terms, all the stimuli that humans and nonhuman animals encounter can be thought of as presaging the possibility of either fitness-decreasing hazards (injury, disease, death, etc.; traditionally termed "punishers" in learning theory and affective neuroscience) or fitnessincreasing resources (food, water, shelter, mates, etc.; "rewards"). Moods and emotions are multifaceted processes for dealing with this; affective states guide physiological, behavioural and cognitive responses to stimuli in order to avoid hazards and obtain resources (Paul, Harding, & Mendl, 2005; Rolls, 2005). The present study is designed to consider the relationship between mood and cognitive responses to potential resources and hazards; specifically, to investigate how mood states influence decisions, and in particular, speed of decisions, about whether ambiguous stimuli predict fitnessincreasing resources or fitness-reducing hazards. Using a computerised task, we test the hypothesis that anxious individuals make decisions that ambiguous stimuli predict hazards more frequently and rapidly than non-anxious individuals and that they make slower decisions that ambiguous stimuli predict resources.

1.1. Anxiety, the Smoke Detector Principle and decision making

In recent years, researchers interested in the evolution of decision making have suggested that many decision-making processes and biases represent functionally appropriate behavioural strategies (e.g., Error Management Theory,

 $[\]stackrel{\text{tr}}{\longrightarrow}$ This research was supported by grants from the Universities Federation for Animal Welfare (UFAW) and the Biotechnology and Biosciences Research Council (BBSRC).

^{*} Corresponding author. Centre for Behavioural Biology, Department of Clinical Veterinary Science, University of Bristol, Langford House, Langford, North Somerset, BS40 5DU, United Kingdom. Tel.: +44 117 331 9071; fax: +44 117 928 9582.

E-mail address: E.Paul@bristol.ac.uk (E.S. Paul).

^{1090-5138/\$ –} see front matter @ 2011 Elsevier Inc. All rights reserved. doi:10.1016/j.evolhumbehav.2010.07.005

Haselton & Buss, 2000; Haselton & Nettle, 2006). For example, in the affective domain, the Smoke Detector Principle, based on Signal Detection Theory (Green & Swets, 1966), predicts that, under conditions of uncertainty, the optimal response to ambiguous, but potentially threatening, stimuli is a defensive one (e.g., flee), even if the probability of actual harm is slight (Marks & Nesse, 1994; Nesse & Williams, 1994; Nesse, 2001; 2005). This is because, as for smoke detectors, the costs of real danger, when it happens, are very high (e.g., death, injury), while the costs of brief but unnecessary defensiveness (e.g., fear, withdrawal, etc.) are relatively small (cf. Dawkins & Krebs, 1979; although this may not always be the case for all species — e.g., see Lima, 1998; Ydenberg & Dill, 1986). This analysis may help us to understand why panic attacks and other anxiety disorders are so common in modern societies, even when actual physical attacks are vanishingly rare. It can also help us to understand when and how treatment for such problems might be best applied (Nesse, 2005).

The Smoke Detector Principle proposes a largely static bias, in which a particular rule of thumb ("if in doubt, respond defensively by withdrawing") is likely to be effective across the lifespans of most individuals (see also Haselton & Nettle, 2006, for other non-affective examples of static biases). But if the costs or probability of harm occurring, or the costs of withdrawal, are subject to changes or differences between or within individuals, the frequency of "false-alarm" defensive responses will also be expected to vary. Indeed, there is considerable trait- and state-based variation in people's tendencies to respond defensively to potential hazards and to interpret ambiguous stimuli as threatening (e.g., Eysenck, Mogg, May, Richards, & Mathews, 1991; Richards et al., 2002). For example, heightened anxiety increases vigilance and attention to potential threats (e.g., Eysenck, 1997; Williams, Watts, MacLeod, & Mathews, 1997) and thereby, presumably, the probability of threat detection (e.g., Byrne & Eysenck 1995). This is because states and longer-term traits of anxiety occur when danger (i.e., the probability of injury, loss, etc.) is heightened (Carver, 2001; Dickson & MacLeod, 2004; Eysenck, Payne, & Santos, 2006); anxiety effectively carries the "information" that the environment is potentially dangerous or threatening (Schwarz & Clore, 1983). Consistent with this, a number of recent studies have found that elevated anxiety shifts the balance of threat-related decisions towards an increased rate of false alarms (i.e., identify threat when it is not in fact present; Becker & Rinck, 2004; Windmann & Kruger, 1998; Winton, Clarke, & Edelmann, 1995). So, the general rule of the Smoke Detector Principle in relation to threat appears to be modulated according to the affective state and/or trait of the person concerned. Here, we test this experimentally by investigating whether anxious individuals are more likely than less anxious ones to judge ambiguous stimuli as predictive of the imminent arrival of hazards and not resources. We also investigate a novel

prediction that the temporal course of such decisions is related to anxiety state.

1.2. Decision-making speed

The Smoke Detector Principle predicts biases in the direction of decisions (e.g., deciding whether something positive or negative is about to happen), but does not make explicit predictions about decision speed. Many attackers (e.g., predators, social adversaries) are likely to strike quickly, to maximise their own chances of successful action (e.g., see Cresswell, 1996). So individuals potentially on the receiving end of such an attack would be wise to respond more rather than less quickly, if they are going to respond at all (Dijksterhuis & Aarts, 2003; Kahneman & Tversky, 1984; Robinson, 1998). Consequently, we propose that, for optimal responsiveness to potentially imminent hazards, individuals in a vigilant, anxious state (e.g., resulting from living in dangerous environments where the benefits of responding quickly outweigh the increased costs of false positives) should be faster to decide that a stimulus predicts danger than less anxious individuals, even if this leads to potentially less accurate decisions (LeDoux, 1996; Trimmer et al., 2008).

When deciding whether to approach potential resources, the converse trade-off would be predicted. To pursue fitnessincreasing resources successfully, an individual needs to be sure that the probability of threat is low (e.g., social or predatory attack; see Ferrari, Sih, & Chivers, 2009). We therefore propose that an optimal decision during anxiety would involve a slowing of interpretation of stimuli as indicating the presence of a resource. In other words, there would be a tendency to trade speed of judgements for the possibility of increased accuracy, to reduce the chance of a false-negative decision when danger is in fact present. The present study thus investigates whether people's selfreported mood (anxiety) is associated with modulations in the latency to make decisions, as predicted here.

1.3. Measuring anxiety and other mood states

We assess individual variation in naturally occurring anxiety using the Positive and Negative Affect Schedule of Watson, Clark, and Tellegen (1988). The PANAS was developed on the basis of studies of the self-reported cooccurrence of different discrete emotion or mood states (see also Watson & Tellegen, 1985; Watson, Wiese, Vaida, & Tellegen, 1999) which demonstrated that individuals tend to experience two largely independent, core types of emotional feeling: negative activation (NA) and positive activation (PA). NA is involved with defence and defence preparation; it is particularly active when threats and potential threats are perceived, and hence high NA is a useful measure of anxiety (people with high-NA scores report negatively valenced, high arousal feelings such as "nervous", "scared", "jittery", "afraid"). PA, on the other hand, is associated with responses to opportunity and resource anticipation; it is particularly

23

active when new resources are expected or received. People with high-PA scores report positively valenced, highly activated states (e.g., "excited", "enthusiastic"), while those with low-PA scores experience fewer positively valenced states. Despite debate over the merits of the PA/NA distinction in mood measurement, and whether the scales should be regarded as bipolar or unipolar (Carver, 2001; Green & Salovey, 1999; Russell & Carroll, 1999; Tellegen, Watson, & Clark, 1999; Watson & Tellegen, 1999), the idea that humans and other animals share two fundamental, biologically adaptive systems of mood or affect - one that arises in response to situations of opportunity, generating appetitive and approach behaviour, and one that arises in situations of threat, promoting heightened vigilance, escape or withdrawal (roughly corresponding to the NA/PA distinction) — is widely supported (e.g., Carver & Scheier, 1990; Carver & White, 1994; Davidson, 1992; Depue, Luciana, Arbist, Collins, & Leon, 1994; Fowles, 1987; Gray, 1987; Mendl, Burman, & Paul, 2010; Schnierla, 1959). Measuring mood using the PANAS scales therefore offers the opportunity to assess the possible effects of both of these two core systems on participants' decisions and decision speed.

Following the arguments above, we hypothesise that people reporting high-NA states will be more likely to decide that ambiguous stimuli predict hazards rather than resources, compared to low-NA individuals. Similarly, people reporting low-PA scores will have reduced expectations that ambiguous stimuli predict resources and hence will *also* be more likely to make negative decisions about ambiguous stimuli (e.g., Mendl et al., 2010). On the other hand, while we predict that threat-oriented high-NA moods will be associated with shortened latencies to decide that stimuli predict imminent hazards, sadness or loss-related low-PA moods will not (because, unlike high-NA states, such moods are not concerned with potential threats that may require rapid responses). Thus, high-NA and low-PA subjects will show similar biases in decision direction, but not in decision speed.

1.4. Computerised task to investigate decisions about expected resources and hazards

To investigate our hypotheses, we used a novel computerbased task in which participants were required to make a choice between two opposing, evaluative decision options: whether simple spatial stimuli displayed on a computer screen predicted the arrival of either a hazard or a resource. Reinforcement contingencies were designed with ecological validity in mind. In everyday life as well as in evolutionary history, detecting potential threats (e.g., social threat, predation threat) enables individuals to escape or avoid fitness-decreasing dangers, while detecting potentially positive stimuli (e.g., food, social or sexual contact) allows them to gain fitness-increasing resources. Mistakenly identifying a positive stimulus as hazardous results in no gain of resource; mistakenly identifying a hazardous stimulus as a positive one can lead to injury or death. Thus, correct classification of a stimulus (as predicting a resource or hazard) allowed participants to *gain* the resource or *avoid* the hazard. When incorrect, the resource *was not gained* or the hazard *was not avoided*. The majority of test stimuli were clearly predictive of either hazards or resources (unambiguous). However, a smaller number of stimuli were completely ambiguous as to whether they predicted hazards or resources (see Methods). These were used because anxious individuals differ from non-anxious ones particularly in terms of their interpretations of affectively ambiguous stimuli. The relative proportion of ambiguous stimuli was necessarily small, so that participants did not have the opportunity to learn that these stimuli were randomly associated with subsequent resources/hazards.

2. Methods

2.1. Participants

Participants were 67 (31 male, 36 female) undergraduate students from the University of Bristol. They volunteered for the experiment, which was described as a "computerised perception task", and the chance to win a £20 prize was offered as an incentive.

2.2. Task materials

The task was presented using the Presentation stimulus delivery and experimental control software (version 0.55, http://nbs.neuro-bs.com), using bitmap stimuli on a black background using CorelDraw 9. The programme was presented to each participant on a 15-in. flat screen monitor (Viglen EZX-15F) at a resolution of 1024×768 pixels.

2.3. Task design

Within each trial, sequentially paired images were presented on the computer screen. The first was a horizontal line 8.7 cm long, with a \odot image at one end and a \odot at the other, as anchor points. The ends of the line at which the \odot and \odot were placed remained constant for individual participants, but were counterbalanced between participants, so half saw the \odot on the left-hand side of the line and the other half saw it on the right. This first image could appear in any one of the four quadrants of the computer screen and was shown for 3 s. The second of the pair of images was the stimulus, a cross (×) which appeared immediately after the first disappeared, in a position somewhere on the line that was now no longer visible. This cross remained on the screen until the participant made a response.

2.4. Reinforcement contingencies

Participants were required to judge whether the stimulus (\times) had appeared in a position on the first image (the line) which was nearer to where the \odot anchor point or the \odot anchor point had been. Responses were made by pressing

Table 1 Response contingencies

Type of trial	\times is closest to:	Participant's response	Correct or incorrect	Reinforcing picture	Points gained or lost
Resource	0	© RES	Correct	Pleasant	+10
Resource	\odot	⊜ HAZ	Incorrect	No picture	0
Hazard	\otimes	© RES	Incorrect	Unpleasant	-10
Hazard	\otimes	⊜ HAZ	Correct	No picture	0
Ambiguous	Neither	© RES	N/A	Pleasant or	+10 OR -10
				unpleasant (random)	(random, as picture)
Ambiguous	Neither	☺ HAZ	N/A	No picture	0

Trial type indicates where the \times was located relative to the \odot and \odot symbols. If the participant responded by pressing the \odot key, this was termed a "resource" (RES) response. Pressing the \odot key was termed a "hazard" (HAZ) response. Reinforcement and points gained/lost depended on whether the response made was correct or incorrect. In the case of ambiguous stimuli, this was determined as shown in the table (see text for further details).

one of two keys on the computer keyboard (J or L), which were labelled
and
, corresponding to the positions (Selft-Sright or Selft-Sright, counterbalanced across subjects) in which they had also appeared on the screen. Reinforcement contingencies were designed with ecological validity in mind (see Table 1 for summary). Judging the × as closer to the \odot was associated with gaining a resource (participants were informed that they would obtain a "reward": a pleasant picture of an animal shown immediately after the response was made, plus a gain of 10 points), while correctly judging it to be closer to the \odot was associated with avoiding a hazard (participants were informed that they would "escape punishment" for this: no picture shown following response, no points). Judging the \times to be closer to the \odot when it was actually closer to the \odot was associated with a hazard (described as a "punishment" to participants: an unpleasant picture of an aggressive or threatening animal shown immediately the response was made, and a loss of 10 points), while incorrectly judging it to be closer to the 🐵 when it was actually closer to the \odot was associated with missing a resource (described as the omission of a reward: no picture shown following the response, and no points).

2.5. Validation of pleasant and unpleasant pictures

The affective qualities of the pictures used were established prior to the experiment in a pilot study. Initially, a panel of six judges rated a set of pre-selected photographic images of animals on a scale of 1-5 (extremely pleasant to extremely unpleasant); concordance between judges was high (Kendall's coefficient of concordance, W=0.147, df=5, p < .001), and three groups of 12 images were generated: "unpleasant" (mean rating >4), "neutral" (mean rating 2-4) and "pleasant" (mean rating ≤ 2). Twelve student volunteers then viewed these 36 images on a computer screen, in a randomised block design (12 block of three images, one of each category, shown for 5 s, with 15 s intertrial interval), while their skin conductance responses on the non-dominant hand were measured using PSYLAB apparatus (Contact Precisions Instruments). A one-way ANOVA demonstrated a significant main effect of stimulus type (pleasant, unpleasant, neutral) on skin conductance response ($F_{2,20}$ =4.50, p<.05).

Post hoc tests revealed that this was accounted for by significantly greater skin conductance responses (i.e., higher arousal) to the unpleasant than to pleasant images (Fisher's least significant difference test, p<.05).

2.6. Procedure

All instructions were given on screen. Participants were first asked their age and sex, and then proceeded to complete a computerised version of the PANAS mood measure (Watson et al., 1988), using keys 1 to 5 to indicate to what extent they currently felt each of 20 emotion states "right now". Participants were then given instructions on how to complete the task (see Section 2.4 above). Each trial consisted of a presentation of the paired stimuli followed by a response from the participant. The relevant pleasant or unpleasant picture (or no picture) and the participants' updated points totals were then displayed for 3 s. The participant who gained the most points in the task won a £20 cash prize.

The task started with eight randomly ordered practice trials with feedback. During four of these practise trials, the stimulus crosses (×) appeared unambiguously closer to the O by at least 11% of the total length of the line, while in another four, they were closer to the O by at least 11%. Responses classifying the stimuli as predictive of "resources" (stimulus closest to O) and "hazards" (stimulus closest to O) were automatically recorded by the computer. Response latencies were also recorded.

Thirty-six experimental trials followed the practise trials, also in randomised order. On 12 of these trials the stimulus × appeared closer to the [©] by at least 11% (unambiguous resource stimulus), on 12 trials it appeared closer to the [©] by at least 11% (unambiguous hazard stimulus) and on another 12 it appeared exactly half way along the line (ambiguous stimulus). These ambiguously positioned stimuli were designed as probe stimuli, to assess participants' tendencies to opt for a positive or negative interpretation when given insufficient information to make a correct evaluation of a stimulus. "Resource" (RES) responses to ambiguous stimuli were randomly reinforced (i.e., RES responses were immediately followed by a 50% probability of either a pleasant animal picture and a gain of 10 points, or an unpleasant animal picture and a loss of 10 points), while "hazard" (HAZ) responses were immediately followed by a grey screen (no picture) and no points lost or gained (see Table 1).

3. Results

3.1. Descriptive statistics

For the purposes of brevity, we describe decisions that the stimulus was nearer the \odot (i.e., that resources and not hazards were anticipated) as "RES" decisions and decisions that the stimulus was nearer the \odot (i.e., that hazards and not resources were anticipated) as "HAZ" decisions. Because mood scores and latencies were normally distributed, parametric analyses were used throughout: Pearson's product moment coefficient correlations and Student's *t* tests.

The PANAS scale yields two mood scores: positive activation (PA) and negative activation (NA). As expected from previous studies, there was no correlation between participants' PA and NA scores (Pearson's r=-0.03, n=67, p=.841). Mood was associated with neither the sex (PA: $t_{65}=0.397$, p=.693; NA: $t_{65}=0.298$, p=.767) nor the age of participants (PA: Pearson's r=0.22, n=67, p=.073; NA: Pearson's r=-0.03, n=67, p=.830).

Participants did not have difficulty classifying the unambiguous stimuli (RES stimuli, nearer to the \odot , 98.6% correct; HAZ stimuli, nearer to the \odot , 94.5% correct). They were significantly faster to classify unambiguous stimuli than ambiguous stimuli (RES: mean ambiguous latency 1094 ms, mean unambiguous latency 725 ms, t_{65} =-6.90, p<.001; HAZ: mean ambiguous latency 1071 ms, mean unambiguous latency 739 ms, t_{65} =-9.14, p<.001), and unambiguous stimuli showed smaller variation (standard deviations, RES: ambiguous 739 ms, unambiguous 320 ms; HAZ: ambiguous 495 ms, unambiguous 298 ms). They did not, however, differ in their speed of classifying ambiguous or unambiguous stimuli as either RES or HAZ (ambiguous RES vs. HAZ: t_{64} =0.28, p=.778; unambiguous RES vs. HAZ: t_{66} =-1.40, p=.167).

There was a non-significant tendency for participants to classify ambiguous stimuli as RES (i.e., nearer to the \odot end of the line) in more than 50% of trials (t_{66} =1.87, p=.066). The proportion of RES responses made to ambiguous stimuli was not significantly associated with either sex (t_{65} =0.07, p=.946) or age (Pearson's r=0.14, n=67, p=.254).

3.2. Relationships between mood and decision direction and speed

PA was positively correlated with the proportion of RES responses made to ambiguous stimuli (Pearson's r=0.33, n=67, p<.01), and NA was negatively correlated with the proportion of RES responses made to ambiguous stimuli (Pearson's r=-0.43, n=67, p<.001).

NA scores were positively correlated with latencies to classify ambiguous stimuli as RES (Pearson's r=0.30, n=66, p<.05; see Fig. 1A); they were also positively correlated with latencies to classify unambiguous stimuli as RES (Pearson's r=0.30, n=67, p<.05; see Fig. 1B). These significant correlations remained even when unusually fast and slow outlier responses were removed from the analyses (± 2.5 S.D. from each individual's mean latency to respond to the three stimulus categories RES, HAZ and ambiguous) (Pearson's r=.31, n=66, p<.05; Pearson's r=.30, n=67, p<.05, respectively). NA scores were not correlated with latencies to classify ambiguous stimuli as HAZ (Pearson's r=0.06, n=67, p=.631), nor with latencies to classify unambiguous stimuli as HAZ (Pearson's r=0.15, n=67, p=.227).

PA scores were not significantly associated with latencies to classify ambiguous stimuli (RES: Pearson's r=-0.23, n=67, p=.068; HAZ: Pearson's r=0.18, n=67, p=.148) or unambiguous stimuli (RES: Pearson's r=0.11, n=67, p=.390; HAZ: Pearson's r=-0.08, n=67, p=.549).



Fig. 1. (A) Scatterplot of NA scores with mean latencies to make ambiguous RES decisions; (B) scatterplot of NA scores with mean latencies to make correct unambiguous RES decisions.

4. Discussion

Using the PANAS mood variable "negative activation" (NA) as an indicator of individual variation in anxiety, we found that, in line with our predictions, NA scores were positively correlated with the tendency to interpret ambiguous stimuli as heralding hazards rather than resources (i.e., HAZ decisions were more frequent for people reporting higher NA). That is, under conditions of uncertainty, and as predicted by the affective modulation of the Smoke Detector Principle presented in the Introduction, anxious participants in the present experiment were more likely to "err on the side of caution" and anticipate threat of some kind. This adds to previous findings that affective state is associated with variation in cognitive processes such as threat detection and interpretation of potential threats (e.g., Eysenck, 1997; Williams et al., 1997).

We further found that such individuals took longer to decide that stimuli predicted resources and not hazards. For both ambiguous and unambiguous stimuli, NA scores were significantly positively correlated with latencies to decide that resources and not hazards were predicted. This is consistent with our suggestion that, under anxious mood conditions that can reflect an increased probability of danger (e.g., Eysenck et al., 2006; Nesse, 2001; 2005), an optimal system would be expected to slow the speed at which it decides that a stimulus predicts a fitness-increasing opportunity and not a threat, in order to achieve a potential increase in accuracy (i.e., to avoid false-negative decisions — that no threats are present when in fact they are). It also parallels previous findings that anxious individuals show delayed attentional disengagement from potential threat signals (e.g., unpleasant words, angry faces) (Fox, Russo, & Dutton, 2002; Fox, Russo, Bowles, & Dutton, 2001). Thus, it may be the case that participants with heightened NA take more time to make positive decisions (that stimuli predict resources and not hazards), because, during evolutionary history, it has been particularly important for individuals in such states to be cautious, making sure that their decisions will not endanger them (Haselton & Buss 2000; Haselton & Nettle 2006). At the very least, the present finding that NA mood states were significantly associated with latencies to make such decisions indicates that the decision mechanism(s) used is open to temporal modulation. Whether NA moods are causally involved in this modulation, and whether actual speed-accuracy tradeoffs are affected by it, remains to be investigated, as it was not possible to gauge accuracy of response to the ambiguous stimuli used in the present task.

In the context of anxiety, we hypothesised that an optimal system would trade accuracy for speed when deciding that hazards were predicted (i.e., the opposite of our hypothesis for decisions predicting resources). However, no evidence for this was demonstrated in the present study; variations in NA were not associated with speed of decisions (either ambiguous or unambiguous) that stimuli predicted hazards. This may be because the participants reporting relatively high NA in this experiment were simply not anxious enough to show this effect (mean NA scores for the whole sample were 14.93, out of a potential maximum score of 50), or the "hazards" used (threatening animal images and loss of points) were not aversive enough. Another possible explanation concerns the experimental design itself: varying the speed at which decisions were made that a stimulus predicted a hazard did not, within this experimental design, directly affect the individual's chances of escaping that hazard, because the affective outcomes were only delivered after the decision was made. So sacrificing accuracy for speed offered no actual advantage. A modification could be made to the task, by adding a random element, in which the hazards could be delivered even without a decision from the participant, at any time point following the commencement of each trial. If affective states were only found to be associated with modulations of decision time in such timerandom tasks, our proposal that high-NA moods may have a generalised influence on hazard-relevant decision times would not be supported; instead, a more local, task-relevant modulation would be indicated.

The self-reported mood variable that we considered as a contrast case to high NA was low PA. High-PA scores represent interested, enthusiastic and excited states, while low scores represent the absence of such positive feelings (e.g., the sad or depressed states associated with absence or loss of fitness-increasing events or resources; see Carver, 2001; Mendl et al., 2010, for support of bipolar formulations of PA/NA-like core affective systems). Such states have been suggested to be valuable to individuals in low opportunity environments, as they protect against fruitless energy expenditure, although they may also be pathologically self-perpetuating, particularly within the social context (Nesse, 2000; Nettle, 2009). Of interest here was whether the relatively negative state of low PA would, like high NA, be associated with pessimistic expectations (i.e., tending to anticipate hazards and not resources), but not with temporal modulations of hazard and resource-related decisions. This was borne out in our findings: individual variations in PA were significantly negatively correlated with the proportion of negative decisions made about ambiguous predictor stimuli (i.e., individuals with low PA were more likely to predict hazards than resources), but not with the speed at which such decisions were made. Obviously, we cannot conclude that the PA variable is never associated with the speed at which negative interpretative decisions are made. Nevertheless, a possible interpretation is that the "pessimistic" association found between low PA and decisions made was primarily concerned with a decreased expectation of resources (i.e., decreased probability or value of resources), rather than an enhanced expectation of hazards, in response to the ambiguous predictor stimuli (MacLeod et al., 1997). We have no *a priori* reasons for expecting the PA variable to be involved in the temporal modulation of resource- and hazard-focused decisions, and our current findings are consistent with this view.

The present experiment offers partial empirical support for our proposed extension of the Smoke Detector model of threat detection and response in humans. By showing that high-NA (anxious) individuals tend to make fewer and slower decisions that stimuli predict resources and not hazards, we can conclude that mood state is in some way associated with the biasing and temporal modulation of such decisions. Nevertheless, our current experimental design includes a number of limitations. Further research will need to be conducted to establish whether this finding represents a true speed-accuracy trade-off, and whether anxiety plays a causal role in the process. In addition, further studies, using a wider variety of participant populations (e.g., representative adult samples, clinical samples, non-Western samples, etc.), will be required to establish the broader applicability and robustness of our findings (Henrich, Heine, & Norenzayan, 2010). Experimental designs using real-life hazards and resources of some kind will also be necessary to establish the ecological validity of our claims. For the present, our results indicate that the neural mechanisms underlying decisions about how to respond to potentially resource- and hazard-predicting stimuli are likely to be affectively modulated and that this modulation incorporates a temporal element, albeit not as fully as we initially suggested. Models for exploring the mechanisms required for such processes have been suggested by a number of researchers in recent years and include signaldetection approaches, as well as others that incorporate a temporal component such as diffusion models (Bogacz, 2007; Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006; Ratcliff & Rouder, 1998; Ratcliff, & Smith, 2004; Ratcliff, 2002; Trimmer et al., 2008).

While much of the history of emotion and mood research has focused on proximate causes, mechanisms and consequences, there is now a growing interest in the evolutionary origins of affective states, traits and disorders (e.g., Bless, 2002; Carver, 2003; McGuire & Troisi, 1998; Öhman & Mineka, 2001). Although this can inevitably be a problematic pursuit [e.g., see Ketelaar & Clore's, 1997 discussion of the difficulties of disentangling proximate effects from ultimate functions in the domain of emotion-cognition interactions], an important advantage of investigating emotion from the perspective of biological systems that have been subject to natural selection is the potential for generating hypotheses about psychological processes or mechanisms that may not otherwise have been considered. The hypotheses we have considered here can be regarded in this light. By proposing an optimal model of threat detection, Nesse's (2005) Smoke Detector Principle has inspired experimentalists to ask fresh questions about the processes involved in threat-related decision making. We hope that by continuing to generate such hypotheses about the possible cognitive influences of affective states, and exploring these experimentally, novel information concerning the processes by which affective states impinge on behavioural decisions will be generated. These, in turn, may have applications in the diagnosis and treatment of affective disorders (see Nesse, 2005, for discussion of practical applications of such approaches) and other areas of behavioural research where performance might be influenced by anxiety, such as occupational psychology and sports psychology.

Acknowledgments

We are grateful to Alex Margetts and James White for their work on a previous version of these experiments. We would also like to thank Rafal Bogacz, Alasdair Houston, James Marshall, John McNamara and Pete Trimmer for many invaluable discussions concerning optimal decision making and the modelling of speed–accuracy tradeoffs. We are also very grateful to the students who participated in the experiment.

References

- Becker, E. S., & Rinck, M. (2004). Sensitivity and response bias in fear of spiders. *Cognition and Emotion*, 18, 961–976.
- Bless, H. (2002). Where has the feeling gone? The signal function of affective states. *Psychological Inquiry*, 13, 29–31.
- Bogacz, R. (2007). Optimal decision-making theories: Linking neurobiology with behaviour. *Trends in Cognitive Science*, 11, 18–125.
- Bogacz, R., Brown, E., Moehlis, J., Holmes, P., & Cohen, J. D. (2006). The physics of optimal decision-making: A formal analysis of models of performance in two-alternative forced choice tasks. *Psychological Review*, 113, 700–765.
- Byrne, A., & Eysenck, M. W. (1995). Trait anxiety, anxious mood, and threat detection. *Cognition & Emotion*, *9*, 549–562.
- Carver, C. S. (2001). Affect and the functional bases of behaviour: On the dimensional structure of affective experience. *Personality and Social Psychology Review*, 5, 345–356.
- Carver, C. S. (2003). Pleasure as a sign you can attend to something else: Placing positive feelings within a general model of affect. *Cognition and Emotion*, 17, 241–261.
- Carver, C. S., & Scheier, M. F. (1990). Origins and functions of positive and negative affect — a control process view. *Psychological Review*, 97, 19–35.
- Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioural activation, and affective responses to impending reward and punishment: The BIS/BAS scales. *Journal of Personality and Social Psychology*, 67, 319–333.
- Cresswell, W. (1996). Surprise as a winter hunting strategy in sparrowhawks Accipiter nisus, peregrines Falco peregrinus and merlins F. columbarius. Ibis, 138, 684–692.
- Davidson, R. (1992). Emotion and affective style: Hemispheric substrates. *Psychological Science*, 3, 39–43.
- Dawkins, R., & Krebs, J. R. (1979). Arms races between and within species. Proceedings of the Royal Society of London, Series B, 205, 489–511.
- Depue, R. A., Luciana, M., Arbist, P., Collins, P., & Leon, A. (1994). Dopamine and the structure of personality: Relation of agonist-induced dopamine activity to positive emotionality. *Journal of Personality and Social Psychology*, 67, 485–498.
- Dickson, J. M., & MacLeod, A. K. (2004). Anxiety, depression and approach and avoidance goals. *Cognition and Emotion*, 18, 423–430.
- Dijksterhuis, A., & Aarts, H. (2003). On wildebeests and humans: The preferential detection of negative stimuli. *Psychological Science*, 14, 14–18.
- Eysenck, M. W. (1997). *Anxiety and cognition: a unified theory*. Hove: Psychology Press.

- Eysenck, M. W., Mogg, K., May, J., Richards, A., & Mathews, A. (1991). Journal of Abnormal Psychology, 100, 144–150.
- Eysenck, M. W., Payne, S., & Santos, R. (2006). Anxiety and depression: Past, present and future events. *Cognition and Emotion*, 20, 274–294.
- Ferrari, M. C. O., Sih, A., & Chivers, D. P. (2009). The paradox of risk allocation: A review and prospectus. *Animal Behaviour*, 78, 579–585.
- Fowles, D. C. (1987). Application of a behavioural theory of motivation to the concepts of anxiety and impulsivity. *Journal of Research in Personality*, 21, 417–435.
- Fox, E., Russo, R., Bowles, R., & Dutton, K. (2001). Do threatening stimuli draw or hold visual attention in subclinical anxiety? *Journal of Experimental Psychology: General*, 130, 681–700.
- Fox, E., Russo, R., & Dutton, K. (2002). Attentional bias for threat: Evidence for delayed disengagement from emotional faces. *Cognition* and Emotion, 16, 355–379.
- Gray, J. A. (1987). Fear and Stress. Cambridge, UK: Cambridge University Press.
- Green, D. M., & Swets, J. A. (1966). Signal detection theory and psychophysics. New York: Wiley.
- Green, D. P., & Salovey, P. (1999). In what sense are positive and negative affect independent? A reply to Tellegen, Watson and Clark. *Psychological Science*, 10, 304–306.
- Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality* and Social Psychology, 78, 81–91.
- Haselton, M. G., & Nettle, D. (2006). The paranoid optimist: An integrative evolutionary model of cognitive biases. *Personality and Social Psychology Review*, 10, 47–66.
- Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, 33, 61–135.
- Kahneman, D., & Tversky, A. (1984). Choices, values, and frames. *American Psychologist*, 39, 341–350.
- Ketelaar, T., & Clore, G. L. (1997). Emotion and reason: The proximate effects and ultimate functions of emotions. In G. Matthews (Ed.), *Cognitive science perspectives on personality and emotion* (pp. 355–398). (Chapter 8), Amsterdam: North-Holland.
- LeDoux, J. E. (1996). The Emotional Brain. New York: Simon & Schuster.
- Lima, S. L. (1998). Stress and decision making under the risk of predation: Recent developments from behavioural, reproductive, and ecological perspectives. *Stress and Behavior*, 27, 215–290.
- MacLeod, A. K., Tata, P., Kentish, J., & Jacobsen, H. (1997). Retrospective and prospective cognitions in anxiety and depression. *Cognition and Emotion*, 11(4), 476–479.
- Marks, I. M., & Nesse, R. M. (1994). Fear and fitness: An evolutionary analysis of anxiety disorders. *Ethology and Sociobiology*, 15, 247–261.
- McGuire, M., & Troisi, A. (1998). Darwinian psychiatry. Oxford: OUP.
- Mendl, M., Burman, O. H. P., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences* (in press).
- Nesse, R. M. (2000). Is depression an adaptation? Archives of General Psychiatry, 57, 14–20.
- Nesse, R. M. (2001). The smoke detector principle: natural selection and the regulation of defenses. *Annals of the New York Academy of Sciences*, 935, 75–85.
- Nesse, R. M. (2005). Natural selection and the regulation of defenses. A signal detection analysis of the smoke detector principle. *Evolution and Human Behavior*, 26, 88–105.
- Nesse, R. M., & Williams, G. C. (1994). Why we get sick: The new science of darwinian medicine. New York: Vintage.

- Nettle, D. (2009). An evolutionary model of low mood states. *Journal of Theoretical Biology*, 257, 100–103.
- Öhman, A., & Mineks, S. (2001). Fears, phobias and preparedness: Toward an evolved module of fear and fear learning. *Psychological Review*, 108, 483–522.
- Paul, E. S., Harding, E. J., & Mendl, M. (2005). Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience* and Biobehavioral Reviews, 29, 469–491.
- Ratcliff, R. (2002). A diffusion model account of response time and accuracy in a brightness discrimination task: Fitting real data and failing to fit fake but plausible data. *Psychonomic Bulletin Review*, 9, 278–291.
- Ratcliff, R., & Rouder, J. N. (1998). Modelling response time for two-choice decisions. *Psychological Science*, 9, 347–356.
- Ratcliff, R., & Smith, P. L. (2004). Psychology and neurobiology of simple decisions. *Trends in Neurosciences*, 27, 161–168.
- Richards, A., French, C. C., Calder, A. J., Webb, B., Fox, R., & Young A. W. (2002). Anxiety-related bias in the classification of emotionally ambiguous facial expressions. *Emotion*, 2, 273–287.
- Robinson, M. D. (1998). Running from William James' bear: A review of pre-attentive mechanisms and their contributions to emotional experience. *Cognition and Emotion*, 12, 667–696.
- Rolls, E. T. (2005). Emotions explained. Oxford: Oxford University Press.
- Russell, J. A., & Carroll, J. M. (1999). On the bipolarity of positive and negative affect. *Psychological Bulletin*, 125, 3–30.
- Schnierla, T. (1959). An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In M. Jones (Ed.), *Nebaska Symposium on Motivation*, (Vol. 7, pp. 1–420). Lincoln: University of Nebraska Press.
- Schwarz, N., & Clore, G. (1983). Mood, misattribution, and judgements of well-being: Informative and directive influences of affective states. *Journal of Personality and Social Psychology*, 45, 513–523.
- Tellegen, A., Watson, D., & Clark, A. L. (1999). On the dimensional and hierarchical structure of affect. *Psychological Science*, 10, 297–303.
- Trimmer, P. C., Houston, A. I., Marshall, J. A. R., Bogacz, R., Paul, E. S., Mendl, M. T., & McNamara, J. M. (2008). Mammalian choices: Combining fast-but-inaccurate and slow-but-accurate decision-making systems. *Proceedings of the Royal Society: B*, 275, 2353–2361.
- Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality and Social Psychology*, 54, 1063–1070.
- Watson, D., & Tellegen, A. (1985). Toward a consensual structure of mood. *Psychological Bulletin*, 98, 219–235.
- Watson, D., & Tellegen, A. (1999). Issues in the dimensional structure of affect — effects of descriptors, measurement error, and response formats: Comments on Russell and Carroll (1999). *Psychological Bulletin*, 125, 601–610.
- Watson, D., Wiese, D., Vaida, J., & Tellegen, A. (1999). The two general activation systems of affect: Structural findings, evolutionary considerations, and psychobiological evidence. *Journal of Personality and Social Psychology*, 76, 820–838.
- Williams, J. M. G., Watts, F. N., MacLeod, C., & Mathews, A. (1997). Cognitive psychology and emotional disorders. 2nd ed. Chichester: Wiley.
- WindmannS., S., & KrugerT., T. (1998). Subconscious detection of threat as reflected by an enhanced response bias. *Consciousness and Cognition*, 7, 603–633.
- Winton, E. C., Clarke, D. M., & Edelmann, R. J. (1995). Social anxiety, fear of negative evaluation and the detection of negative emotion in others. *Behavior Research and Therapy*, 33, 193–196.
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. Advances in the Study of Behavior, 16, 229–249.